

A NEW FOSSIL CONIFER, *BELLARINEA RICHARDSII*, FROM THE
EARLY CRETACEOUS STRZELECKI GROUP, SOUTHEASTERN VICTORIA

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A new species of fossil conifer foliage, *Bellarinea richardsii*, is described and illustrated from Neocomian (Early Cretaceous) sediments of the Tyers River Subgroup in south-eastern Victoria. The specimens consist of intact seasonal shoots and isolated leaves, and their depositional setting in prominent leaf mats suggests a seasonal, deciduous habit. Individual leaves are spirally inserted on the shoot axis but the leaf bases are twisted to lie on a common plane giving the shoots plagiotropic symmetry. Although lacking attached reproductive structures the gross morphology and cuticular details of the shoots and leaves suggests assignment to either Podocarpaceae or Taxodiaceae. This species and a range of comparable forms represent a prominent component of Australian mid-Mesozoic floras.

Keywords: Palaeobotany, conifer, Early Cretaceous, Strzelecki Group

MESOZOIC FLORAS have been known from Victoria since the pioneering work of McCoy (1874, 1875). Early reports assigned much of this material to the Jurassic (McCoy 1860, 1875, Seward 1904), but for the last 40 years it has been recognized that this component is Early Cretaceous in age (Dettmann 1963, Douglas 1969, 1973). Victorian Cretaceous floras are of interest because the forests that they represent grew at high southern latitudes, experienced conditions unlike any that exist in the world today, and were home to a diverse biota including polar dinosaurs (Rich et al. 1988).

Conifers represented an important component of floras throughout the Victorian Early Cretaceous. Assemblages assigned to Douglas' (1969) Zone A (= *Ptilophyllum spinosum*-*P. castertonensis* Zone: latest Jurassic? to early Neocomian) are known only from bore cores in the Otway Basin and their conifer remains have not been studied in detail. Assemblages referable to Douglas' Zone B (= *Plylopteroides laevis* Zone of Cantrill & Webb 1987: Neocomian) are recorded from the Boola Boola Forest of Gippsland, small areas on the Mornington Peninsula and Philip Island and from the subsurface of the western Otway Basin. Rich plant assemblages from these beds have recently been described by McLoughlin et al. (2002). Assemblages assigned to Douglas' Zone C (roughly equivalent to the *Plylopteroides serrata* Zone of Cantrill & Webb 1987: Barremian to earliest Albian) are widely represented in the Gippsland and Otway

basins. Several taxa of coniferous foliage have been described from this zone including *Bellarinea barklyi* Florin, *Elatocladus mccoysi* Florin, *Elatocladus* sp., *Podozamites ellipticus* McCoy, *Bractyphyllum gippslandicum* McCoy, *Araucaria* sp. cf. *A. heterophylla* (Salisbury) Franco, and a range of cones, cone scales, and seeds mostly with inferred araucarian or podocarpacean affinities (McCoy 1874, Florin 1952, Drinnan & Chambers 1986). Douglas' Zone D (roughly equivalent to the *Plylopteroides dentata* Zone of Cantrill & Webb 1987: Albian) assemblages are confined to the Otway Basin and are rich in conifers. Cantrill & Douglas (1988) and Cantrill (1991, 1992) documented the leaf morphology, cuticular features and phylogenetic affinities of five species ascribed to *Araucaria*, one to *Agathis*, and several broad-leafed forms assigned to the form-genus *Podozamites*. Cantrill (1991) suggested that the *Podozamites* species were possibly representatives of Podocarpaceae or Araucariaceae, and Pole (1995) later transferred *Podozamites taenioides* to *Araucarioides*. Cantrill & Douglas (1988) erected *Geinitzia tetragona* for conifer foliage associated with roots bearing mycorrhizal nodules and suggested a taxodiaceous affinity for this species, but Pole (2000) considered the cuticular micromorphology to be indicative of a cheirolepidiacean affinity and transferred this species to the new genus *Otwayia*.

Assemblages representative of the *Plylopteroides laevis* Zone (Douglas' Zone B) are best

expressed in exposures of the Tyers River Subgroup in the Boola Boola Forest north-northwest of Traralgon (Fig. 1A). This zone is notable for its abundance of small-leaved bennettitaleans (*Otozamites*) and several other pteridosperm taxa [*Taeniopteris daintreei* McCoy, *Rintonlia variabilis* (Douglas) McLoughlin & Nagalingum in McLoughlin et al. (2002), *Komlopteris indica* (Feistmantel) Barbaekaa and *Pachydermophyllum anstropapillosum* (Douglas) McLoughlin & Nagalingum in McLoughlin et al. (2002)], which most likely represented the principal mid-storey elements of the vegetation. Associated with these pteridosperm leaves in the Boola Boola assemblages are abundant conifer leaves belonging to plants that probably constituted the upper stratum of these Early Cretaceous forests. Three principal conifer species are represented: *Brachyphyllum tyersensis* Tosolini & Nagalingum (in McLoughlin et al. 2002), *Otwayia hermata* Tosolini & Nagalingum (in McLoughlin et al. 2002) and a new species of *Bellarinea*, that is the basis of this paper.

GEOLOGICAL SETTING

The Boola Boola Forest is located approximately 12 km north-northwest of Traralgon, Gippsland (Fig. 1A). The rocks exposed in this area represent the northernmost extent of Cretaceous sediments in the Gippsland Basin and they rest on Lower Devonian metasedimentary rocks with an angular unconformity of considerable relief. They are separated from Cretaceous exposures of the South Gippsland Highlands by Cenozoic sediments in the Latrobe Valley Depression. Lower Cretaceous rocks of the Gippsland Basin have been assigned in their entirety to the Strzelecki Group (Douglas 1988). The upper part of the succession is dominated by feldspathic sandstones and has been assigned to the 'Wonthaggi Formation' by Constantine & Holdgate (1993). The lower part of the succession, assigned to the Tyers River Subgroup and principally exposed in the Boola Boola Forest area, is dominated by conglomerates and quartzose or lithic sandstones. The Tyers River Subgroup incorporates the Tyers Conglomerate (c. 120 m thick) and Rintoul Creek Formation (c. 480 m thick) in ascending order (Tosolini et al. 1999). The Rintoul Creek Formation has been further subdivided into a lower unit (Loemany Member) of mixed lithologies and an upper unit (Exalt Member) dominated by thick sandstone packages.

The Tyers Conglomerate is interpreted to represent alluvial fan and proximal braided river deposits whereas the succeeding Rintoul Creek Formation represents mixed braided and meandering river deposits in alluvial valley settings (Tosolini et al. 1999). The material used in this study is from the lower part of the type section of the Rintoul Creek Formation (Loemany Member), approximately 160 m above the base of the unit. Biostratigraphic studies of the sampled beds have assigned these rocks to the *Foraminisporis wonthaggiensis* palynozone (Dettmann 1963, Helby et al. 1987), *Phyllopteroides laevis* macrofloral zone (Cantrill & Webb 1987), and the *Trikonia loemanyensis* megaspore zone (Tosolini et al. 2002) of Neocomian age (Fig. 1B).

MATERIAL AND METHODS

Specimens used in this study were collected over a period of 35 years from the mid-1960s by Dr. J. Douglas (formerly of the Geological Survey of Victoria) and the present authors. The material is derived from several localities in the Boola Boola State Forest, 12 km NNW of Traralgon, Victoria (Fig. 1A). Cuticles were prepared by oxidation in Schultze's solution (nitric acid with dissolved potassium chloride crystals) for up to one hour to remove coalified mesophyll tissues. Slight heating (up to 45°C) and further treatment with 5% sodium hydroxide or 5% ammonia for up to 15 minutes was undertaken in an attempt to clean the cuticle. Despite varied chemical treatments and heating, *B. richardsii* cuticle proved difficult to recover. It is thin and readily fragmented. In most cases, the best detail of the external surface was obtained by scanning electron microscopy of unoxidized leaves (Fig. 2H, I). Recovery of cuticle after oxidation of the coalified mesophyll did not yield fragments large enough to provide significant details of the cuticle's inner surface morphology. Material for scanning electron microscopy was air-dried, attached to stubs using double sided carbon stickers, and sputter coated with gold. All measurements of epidermal features are from dried specimens. Specimens with the prefix MVP are registered with Museum Victoria, Melbourne.

SYSTEMATIC PALAEOBOTANY

Phylum Coniferophyta
Class Coniferopsida
Order Coniferales

Genus *Bellarinea* Florin 1952 emend.

Type species: Bellariuea barklyi Florin 1952; Eumeralla Formation; Aptian; Bellarine Peninsula near Geelong, Victoria, Australia.

Emended diagnosis. As per Florin (1952), but deciduous determinate shoots without branches or terminal resting buds.

Florin (1952) erected *Bellarinea* for shoots with essentially identical gross architecture to those of *Elatocladus* but where cuticular features revealed that the leaves were hypostomatic with haplocheilic stomata arranged in a band on each side of the midvein. Florin's specimens came from Aptian sediments in southern Victoria, and his two species remain the only ones attributed to this genus until this study. *Elatocladus* was erected by Halle (1913) to encompass sterile coniferous shoots of uncertain affinity with spiral phyllotaxy, including those with leaf bases twisted to give a plagiotropic orientation. Halle included in the genus three species from the mid-Mesozoic of India, which he considered identical to the specimens he was describing from the Jurassic Hope Bay locality in west Antarctica. Harris (1979) later emended the diagnosis of *Elatocladus* to incorporate only coniferous shoots that bear linear, univeined leaves that diverge from the stem and are flattened to lie in the same plane. Although this restricted to some extent the morphological scope of the form-genus, it is still sufficiently broad to encompass foliage as different as the rhythmically dimorphic shoots of *Sequoia* (Taxodiaceae), *Cephalotaxus* (Cephalotaxaceae) and *Prumnopitys* (Podocarpaceae), and the seasonally deciduous shoots of *Taxodium* and *Metasequoia* (Taxodiaceae). Unfortunately, Halle's type species, *Elatocladus heterophyllus*, is quite different to most other species of the genus, which have long, narrow, bifacial leaves that are twisted to give the shoot a plagiotropic symmetry. Harris' incorporation of a suite of species from the Jurassic of Yorkshire also substantially expanded the geographical extent of the genus, which was originally Gondwanan. Florin and Harris clearly had different approaches to the use of generic names. Florin preferred smaller genera that were restricted in morphology, and he instituted new genera whenever features were available; Harris preferred broadly circumscribed form-genera and in fact synonymized several of Florin's genera into *Elatocladus* (including one Florin had named for Harris ("*Touharrisia*"). The reason for our choice of an emended *Bellarinea* in preference to *Elatocladus* is to make the distinction

between deciduous shoots (*Bellarinea*) and persistent shoots with rhythmic growth (most *Elatocladus*).

Some Gondwanan Mesozoic conifers with plagiotropic shoots similar to *Bellarinea* and *Elatocladus* have been included in the genera *Mataia* and *Rissikia*. *Mataia* was erected by Townrow (1967) for Jurassic podocarpaceous remains from New Zealand and northeastern Australia. It incorporates shoots bearing hypostomatic to weakly amphistomatic leaves with contracted bases in pseudodistichous arrangement but the genus is defined mainly on reproductive characters that are unavailable for most species of *Bellarinea* and *Elatocladus*. *Rissikia* leaves are rhombic in section with a band of stomates located on each flank. This genus is further differentiated from *Bellarinea* and *Elatocladus* by the presence of small, spirally arranged, scale-like leaves at the base of the shoot proceeded by larger leaves generally in pseudodistichous arrangement. *Rissikia* species are mostly represented in the Triassic of Gondwana and have probable podocarpaceous affinities (Townrow 1967, Anderson & Anderson 1985).

Bellarinea richardsii sp. nov.

Fig. 2A-1

?1958 *Elatocladus* sp. cf. *E. confertus* Halle – Philip, p. 192.

?1958 *Elatocladus uccoyi* Florin – Philip, p. 192.

1969 *Elatocladus* sp. 'a' – Douglas, p. 265.

cf. 1969 *Elatocladus* sp. 'b' – Douglas, p. 90, pl. 9, fig. 2.

1986 *Rissikia* sp. – White, pp. 176, 185, figs 268, 284.

1994 *Elatocladus* sp. – Douglas, p. 178, fig. 9.6a.

Holotype. MVP209942.

Paratypes. MVP209943-209957.

Type locality. Loc. L14 of Douglas (1969), near Exalt Creek, Boola Boola State Forest, central Gippsland, Victoria (Australian Map Grid reference DT045457,578132).

Type formation and age. Loemany Member, Rintoul Creek Formation, Tyers River Subgroup, Strzelecki Group; *Phyllopteroides laevis* macrofloral zone (Cantrill & Webb 1987); Neocomian.

Etymology. After Dr Max Richards, former board member of the CSIRO and chair of the University of Melbourne, School of Botany Foundation.

Diagnosis. Determinate axes bearing up to 45 spirally inserted leaves that are twisted at the base into a pseudo-distichous arrangement. Leaves are univeined, linear to inflexed falcate. Leaf apices are obtuse, commonly possessing a mucronate tip; leaf bases are decurrent. Leaf density is 4–10 per 10 mm. Epidermal cells are rectangular with straight walls. Stomates surrounded by 4–6 papillate subsidiary cells.

DESCRIPTION

Gross morphology. Coniferous shoots up to 84 mm long, consisting of an unbranched, determinate axis bearing up to 45 leaves diverging at 40°–90° to the axis. Leaves are spirally inserted on the axis, but the leaf bases are twisted to give the appearance of a distichous arrangement. The leaves are linear to inflexed-falcate, <16 mm long (typically 5–10 mm) and 0.5–2 mm wide (average 1 mm). Leaf apices are obtuse and commonly mucronate, leaf bases are decurrent, and leaf margins entire. Adjacent margins of leaves on the same side of a shoot are 0.5–4 mm apart, leaf density is 4–10 leaves per 10 mm and the leaves very rarely overlap. The leaves have a mid-vein that extends into the mucronate tip.

Foliar micromorphology. Epidermal cells are more or less rectangular, and orientated along the axis of the leaf forming a brick-like pattern (Fig. 2H, I). The leaf surface has an uneven or slightly verrucate texture due to bulging of the periclinal walls of epidermal cells. Stomates are arranged in two longitudinal bands on the abaxial leaf surface. Stomatal pores are 26–34 µm long and are surrounded by 4–6 weakly developed, roughly circular papillae or lobes that are 9 µm in diameter.

Distribution. Localities L1, L4, L8, L14, L20, L23, L24, L28, L30 (see Douglas 1969 for details); Localities LC1, LC3, RC17B, RC17C, RC17D, RC20A (see McLoughlin et al. 2002 for details); Tyers River Subgroup (Neocomian), Gippsland Basin, Victoria.

COMPARISON AND REMARKS

Morphology. There is considerable variation in leaf dimensions and orientation among the specimens of *B. richardsii*, however, all have a broadly similar architecture consisting of shoots bearing bifacial, univeined leaves with decurrent, twisted, but

unconstricted bases. In a few impressions the leaf bases appear to be contracted but this is due to twisting. Most leaves of *Bellarinea richardsii* are 1 mm wide, linear or very slightly falcate and 2 mm apart. This 'typical' condition was found in over 50 specimens in the Boola Boola fossil flora (Fig. 2A, D, E, F, G). There are several specimens with smaller (1.5–4 mm long) and more closely spaced leaves (10 leaves per 10 mm) but the shoots exhibit the same gross morphology as the 'typical' specimens and are possibly immature or under-developed shoots. Two other unusual specimens have inflexed falcate leaves that are spaced at 4 per 10 mm along the shoot (Fig. 2B), compared to 6–8 leaves per 10 mm in the 'typical' shoots. The range of leaf arching may vary considerably along a single shoot. In many cases, strongly curved leaves are also relatively narrow (Fig. 2B). The margins of extant *Metasequoia glyptostroboides* leaves become recurved with desiccation and this process may have been responsible for the arching, twisting and enrollment of some *B. richardsii* leaves.

Complete shoots of *Bellarinea richardsii* are preserved in densely matted accumulations, which is suggestive of a deciduous habit. The slender axes bear leaves of nearly uniform length supporting the hypothesis that the fossils represent detached short shoots of a single season's growth. The leaves along some shoots of *B. richardsii* decrease in length distally (Fig. 2C), but the general condition is with leaves of roughly the same length along the entire shoot. They are similar in appearance to the entirely abscised shoots of extant *Taxodium distichum* (L.) Richard. However, detached *Bellarinea*-like leaves are also very common in the Boola Boola sediments suggesting that at least some were shed before the shoots abscised. This latter style of foliar detachment is similar to that of extant *Metasequoia glyptostroboides* Miki ex Hu & W.C. Cheng, which often sheds many of its leaves before the shoots. There is no evidence of branching on any of the shoots and none of the specimens possesses axillary or terminal buds. This favours the interpretation that the shoots were seasonally shed units.

Affinities. The systematic affinities of *Bellarinea richardsii* are unclear due to the lack of attached reproductive organs and the difficulty in obtaining definitive cuticular characters. Pollen from several conifer families occurs in the Tyers River Subgroup (Dettmann 1963). Araucariaceae is represented by the pollen *Araucariacites australis* Cookson ex Couper.

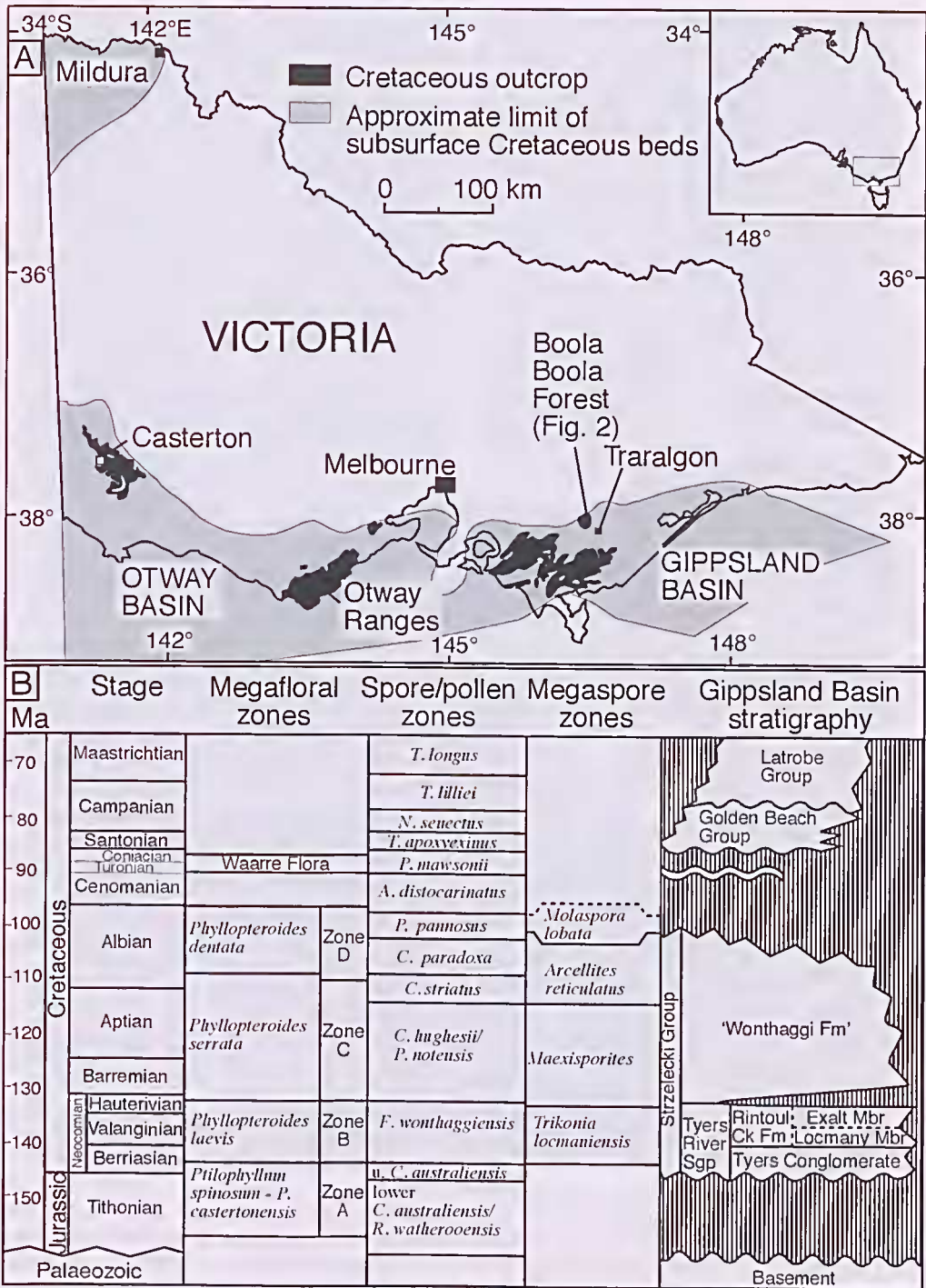


Fig 1. Geographic and stratigraphic position of the fossil beds. A. Map of Victoria showing the distribution of Cretaceous sedimentary rocks and the location of Boola Boola Forest; B. Cretaceous stratigraphy and biozones of the Gippsland Basin. Adapted from Douglas (1969), Cantrill & Webb (1987), Helby et al. (1987), Smith (1988), Tosolini et al. (1999) and Tosolini et al. (2002).

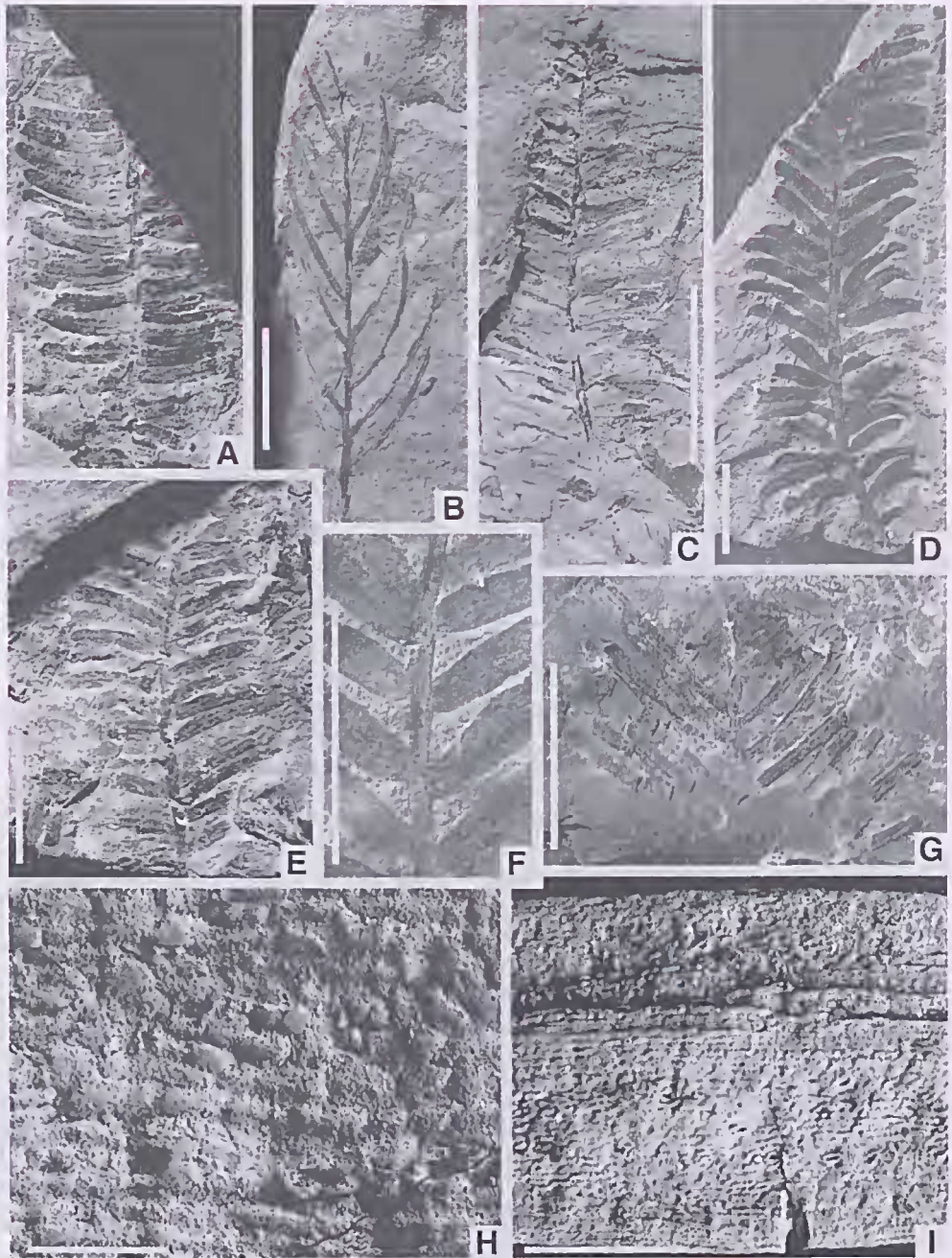


Fig 2. *Bellarinea richardsii*. A. Shoot displaying typical leaf arrangement, MVP209950B, Loc. RC20A; B. Shoot with incurved, narrow, falcate leaves, MVP209943, Loc. RC17D; C. Immature or under-developed shoot with leaves reducing in size towards the shoot apex, MVP209949, Loc. RC17D; D. Shoot displaying typical pseudodistichous leaf arrangement, MVP209942 (holotype), Loc. L14; E. shoot displaying typical leaf arrangement and form, NMVP209950A, Loc. RC20A; F. Enlargement of typical shoot axis showing pseudodistichous, spirally inserted, leaf bases, MVP209942, Loc. L14; G. Shoot with narrow coalified leaves, MVP209948, Loc. RC20A; H. Scanning electron micrograph of MVP209948 showing regular epidermal cells with bulging periclinal walls and stomates with papillae; I. Scanning electron micrograph of MVP209948 showing stomates in longitudinal bands either side of the midvein. Scale bar = 10 mm for A-G; 100 µm for H; 1 mm for I.

However, this pollen is likely to be associated with araucarian cone scales and small, slender twigs bearing appressed, scale-like leaves assigned to *Brachyphyllum tyerseusis* Tosolini & Nagalingum (in McLoughlin et al. 2002). *Brachyphyllum tyerseusis* has wax-filled, obliquely orientated, cycloctytic stomates with four to six subsidiary cells typical of araucariacean leaves. Cheirolepidiacean pollen is represented by *Corollina* sp. cf. *C. torosa* (Reisinger) Klaus. However, it is unlikely that *B. richardsii* is cheirolepidiacean as the leaves of that family are typically scale-like with strongly sunken stomates protected by prominent papillae, and borne in spirals, whorls or opposite-decussate arrangement (Alvin 1982). Specimens attributed to *Otwayia hermata* Tosolini & McLoughlin (in McLoughlin et al. 2002) from the Boola Boola assemblage show these foliar features and are the likely affiliates of the *Corollina* pollen. Podocarpaceae is represented by pollen referable to *Podocarpidites* sp. cf. *P. ellipticus* Cookson and *Microcachyridites antarcticus* Cookson. Taxodiacean/cupressacean pollen is unknown from these deposits and has only been regularly reported in post-Cretaceous sediments in Australia (Macphail et al. 1994). Nevertheless, taxodiacean macrofossils are known from the mid-Cretaceous (Peters & Christophel 1978) suggesting that the early pollen record of this group has been overlooked on this continent. Small asulcate grains such as those referred to *Spheripollenites*, although not recorded from Boola Boola, are found elsewhere in the Victorian Early Cretaceous, and these are not unlike the pollen of extant Taxodiaceae. Florin (1963) argued that most *Elatocladus*-type shoots from the Southern Hemisphere, including *Bellarinea*, were probably podocarpaceous but the dearth of consistently distinctive architectural or cuticular characters separating Taxodiaceae and Podocarpaceae foliage and the absence of reproductive remains associated with the Boola Boola fossils prevents definitive familial assignment of *B. richardsii*.

Leaves of *B. richardsii* are basally twisted, which results in a distichous appearance (Fig. 2F). This leaf arrangement is common among some extant and fossil Taxodiaceae (e.g., *Metasequoia*, *Taxodium* and *Sequoia*) and Podocarpaceae (e.g., *Falcatifolium*, *Afrocarpus*, *Nageia*, *Retrophyllum*, *Prumnopitys*, *Daercarpus*, *Acmopyle*, *Mataia*, *Smithtonia*, and *Willungia*). Those extant Taxodiaceae with linear leaves in pseudodistichous arrangement are mostly deciduous and have thin cuticle with either a smooth surface (*Taxodium*: Alvin & Boulter 1974, Sung Soo Whang & Hill 1999) or

with a uneven surface caused by lobing of the periclinal walls of epidermal cells (*Metasequoia*: Qin Leng et al. 2001). Some Taxodiaceae lack Florin rings (e.g., *Sequoia*, *Cunninghamia*) but others (e.g., *Metasequoia*, *Athrotaxis*) have Florin rings that are typically lobed (Oladele 1983). Stomata of linear-leaved Taxodiaceae, such as *Metasequoia*, generally have apertures orientated parallel to the leaf axis, strongly cutinized guard cells, and around 4–6 subsidiary cells that are not strongly differentiated from surrounding epidermal cells. The cuticle of *B. richardsii* is thin, and very difficult to prepare compared to co-fossilized Bennettitales and other conifers; this thin cuticle is further evidence for a deciduous habit. Its stomata are axially aligned and the subsidiary cells are, at best, only weakly raised. Some podocarp genera, such as *Falcatifolium* and *Retrophyllum*, produce short shoots with a pseudodistichous array of bifacial leaves whereas others, such as *Daercarpus* and *Acmopyle*, show similar twisting at the base of leaves but the leaves are bilaterally flattened. *Bellarinea richardsii*, with symmetrical bands of stomata restricted to the abaxial surface appears to possess bifacial leaves. Most Podocarpaceae have smooth cuticle but some possess low papillae, irregular ridges, or the epidermal cells have an inflated appearance or verrucate texture (Hill & Polc 1992). In many cases podocarps have prominent Florin rings around the stomates but in some cases (e.g., *Smithtonia* and *Willungia*) these may be poorly developed or divided into irregular lobes. All extant Podocarpaceae are evergreen, and most have a relatively robust cuticle. Possession of a distinct abaxial stomatal band on either side of the midvein, longitudinally aligned, slightly inflated epidermal cells, and weakly papillate subsidiary cells, is consistent with Florin's (1952) placement of *Bellarinea* in Podocarpaceae but an affinity to Taxodiaceae can not be excluded.

Comparisons with other mid- to late Mesozoic conifer fossils

Several conifer fossils with similar gross morphology to *B. richardsii* have been recorded from Australian Jurassic-Cretaceous strata (Table 1). These have been variously assigned to the form-genus *Elatocladus*, or to genera with implied cuticular or reproductive affinities to modern conifer families. All of these fossils differ to a greater or lesser degree to the specimens here assigned to *B. richardsii*.

Although Douglas (1969) did not describe any conifers from the Victorian Lower Cretaceous he listed '*Elatocladus* sp. a' in the Boola Boola fossil flora. These remains are probably conspecific with *B. richardsii* given the appearance of *Elatocladus* remains from this flora that he illustrated in later studies (Douglas 1994). Douglas (1969) also figured the apex of a conifer leaf assigned to '*Elatocladus* sp. b' from Boola Boola. However, this illustration does not have sufficient detail to assess its affinity with *E. richardsii*. As part of an investigation into the sedimentology of the Tyers River Subgroup, Philip (1958) listed the presence of *Elatocladus* sp. cf. *E. confertus* and *E. mccoysi*, but these identifications were not supported by illustrations or descriptions.

Stirling (1892, 1900) assigned *Elatocladus*-like shoots from Aptian of the Gippsland Basin to *Palissya australis* McCoy. These shoots exhibit rhythmic growth of the leaves along their length, but differ from *B. richardsii* by having either spirally arranged leaves (Stirling 1892, Parris et al. 1995) or pseudodistichous leaves borne on shoots with multiple branches (Stirling 1900). At least some of these leaves also differ from *B. richardsii* in having bilaterally flattened leaves (see Parris et al. 1995, fig. 8a). The *Palissya australis* specimens were later transferred to *E. confertus* by Arber (1917) and considered synonymous with New Zealand, Antarctic and Indian specimens (Arber 1917, Sahni 1928). Medwell (1954) assigned several Victorian specimens to *E. confertus* but they were not figured or described and the specimens cannot be located. Townrow (1967) later re-assigned Arber's specimens of *E. confertus* to *Mataia podocarpoides* Townrow because they exhibited irregular branching whereas the Antarctic type material has more or less pinnate branching. *Mataia podocarpoides* is further distinguished from *B. richardsii* by the possession of attached ovuliferous cones (Townrow 1967).

Elatocladus mccoysi was described by Florin (1952) based on an Aptian specimen from the Otway Basin. The leaves of both *B. richardsii* and *E. mccoysi* are borne spirally but twisted to give a distichous appearance. The lengths of some *B. richardsii* leaves fall within the size range of *E. mccoysi*, however, the two species are regarded as distinct because the leaves of the former are typically linear to oblong and straight to inflexed, whereas leaves of the latter are lanceolate to falcate and strongly reflexed. An additional Aptian specimen from the Otway Basin was assigned to *Elatocladus* sp. by Florin

(1952) but this shoot has spirally arranged, 2.5–4.5 mm long, triangular leaves and should be transferred to *Pagiophyllum* or *Otwayia*.

Aptian twigs from the Gippsland and Otway basins assigned to *Bellarinea barklyi* have pseudodistichous leaves with decurrent bases (Florin 1952, Drinnan & Chambers 1986). This species has bifacial leaves 14–32 mm long and 1.8–3 mm wide. Most leaves of *B. richardsii* are slightly smaller than those of *B. barklyi*. The stomates of both *B. barklyi*, known only from the Aptian, and *B. richardsii*, recorded only from the Neocomian, are arranged in two longitudinal bands but the former is distinguished by having sinuous-walled epidermal cells in the non-stomatiferous areas.

Elatocladus planus (Feistmantel) Seward has been recorded from numerous Gondwanan Jurassic-Cretaceous localities (Townrow 1967). In Australia, *E. planus* has been described from the Talbragar flora of New South Wales (Walkom 1921), Algebuckina Sandstone, South Australia (Glaessner & Rao 1955) and several Mesozoic formations of Queensland (Walkom 1917, 1919). It is not clear that all, or any, of the Australian forms referred to this species are conspecific with the Indian type material. Townrow (1967) noted that this species 'almost certainly will prove to be composite' upon further investigation. This suggestion proved correct in the case of the ?Middle Jurassic Talbragar specimens, which were later reassigned to *Rissikia talbragarensis* White 1981. The Talbragar species differs from both *E. planus* and *B. richardsii* on the basis of its more closely spaced, longer leaves with distinct transverse striations (White 1981). Townrow (1967) excluded the South Australian specimens from his synonymy list for *E. planus*. McLoughlin (1996) suggested that the South Australian *E. planus* (Glaessner & Rao 1955) specimens may be synonymous with *Elatocladus ginginensis* McLoughlin but could not confirm their identity as the former are ill-preserved. *Bellarinea richardsii* is broadly similar in morphology and size to *Elatocladus ginginensis* from the Neocomian-Barremian of Western Australia (McLoughlin 1996). The latter has leaves with variably contracted or decurrent bases. Its leaves are distally tapered but lack a mucronate tip. In contrast, *B. richardsii* has leaves with a mucronate apex and decurrent bases that are not contracted. *Elatocladus*-like shoots originally described by Walkom (1918) from the Lower Cretaceous of Queensland have subsequently been assigned to a new species,









Characters	 <i>B. richardsii</i>	 <i>B. barklyi</i>	 <i>E. planus</i>	 <i>E. mccoysi</i>	 <i>E. talbragarensis</i>	 <i>E. ginginensis</i>	 <i>E. baddowensis</i>	 <i>M. podocarpoides</i>
Shoot length	84 mm	c. 100 mm	>90 mm	>25 mm	127 mm	51 mm	>41 mm	30 mm; shoots commonly retained in connection with parent shoots
Leaf arrangement	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous	spiral; basally twisted to pseudodistichous; opposite-subopposite	spiral; basally twisted to be more or less distichous except near base of ultimate shoots where they remain spiral
Maximum leaf length	16 mm	32 mm	26 mm	11 mm	c. 60 mm	20 mm	17 mm	15 mm
Maximum leaf width	2 mm	3 mm	1.2 mm	1 mm	2 mm	1 mm	2.5 mm	4 mm
Leaf shape	linear; straight, inflexed or reflexed	linear to lanceolate	linear; commonly reflexed	linear; generally reflexed	linear; in some cases slightly reflexed or inflexed	linear; in some cases slightly reflexed or inflexed	oblong to lanceolate; straight or slightly inflexed	oblanceolate; commonly reflexed
Leaf orientation	40-90° from axis	40-90° from axis	60-90° from axis	50-75° from axis	20-90° from axis	35-60° from axis	45-90° from axis	40-80° from axis
Leaf cross-section	uncertain probably flat or slightly keeled	uncertain; probably keeled	uncertain; probably keeled	uncertain; probably keeled	uncertain; probably keeled	uncertain; probably keeled	uncertain; probably flattened	triangular; strongly keeled below midvein
Leaf base	twisted, broadly decurrent	slightly contracted, non-petiolate, twisted, strongly decurrent	not significantly contracted, strongly decurrent	slightly contracted, twisted, broadly decurrent	in most cases markedly decurrent (specimens with transverse striae on leaves here excluded)	slightly contracted, non-petiolate, twisted, slightly decurrent	slightly contracted weakly decurrent	tapered; markedly decurrent
Leaf apex	obtus, commonly mucronate	subacute to obtuse	acutely pointed to rounded	acute to almost obtuse	blunt obtuse or rounded	rounded or blunt obtuse	rounded or blunt obtuse	variable; rounded, acute, or slightly mucronate
Stomatal distribution	hypostomatic; 0.3 mm broad stomataliferous band in centre of lamina either side of midvein	hypostomatic; 0.5 mm broad stomataliferous band in centre of lamina either side of midvein	not available	not available	not available	not available	not available	hypostomatic or very unequally amphistomatic; stomata restricted to zones in uncertain position
Arrangement of stomates	erranged in at least two longitudinal files; apertures longitudinally orientated	haplocheilic stomates with mostly oblique apertures in weakly defined longitudinal rows	not available	not available	not available	not available	not available	monocyclic; arranged in longitudinal, though often irregular rows apertures mostly longitudinally orientated
Subsidiary cells	papillate	4-6; never shared, slightly papillate; slightly raised to form weak Florin ring	not available	not available	not available	not available	not available	4-6; never shared but sometimes adjacent; bearing hemispherical papillae; Florin ring absent
Guard cells	sunken	slightly sunken	not available	not available	not available	not available	not available	slightly sunken
Papillae	present, only on subsidiary cells	present only on subsidiary cells	not available	not available	not available	not available	not available	generally present only on subsidiary cells
Epidermal cells	rectangular	generally rectangular or with slightly sinuous anticlinal walls	not available	not available	not available	not available	not available	mostly rectangular with slightly sinuous anticlinal walls
Affiliated reproductive structures	no obvious associated fruits	no obvious associated fruits	no obvious associated fruits	no obvious associated fruits	associated with 120 mm long cones comprised of c. 30 spirals of cone scales each bearing a ?solitary seed	no obvious associated fruits	no obvious associated fruits	seed cone spike-like; 30 mm long; bearing 8-12 spirally arranged units comprising a bract and axillary ovuliferous scale bearing two stalked seeds
Type formation or locality	Rintoul Creek Formation, Gippsland Basin, Australia	lower Eumeralla Formation, Olway Basin, Australia	Vemavaram Formation Craveery-Palar Trough, India	lower Eumeralla Formation, Olway Basin, Australia	Purlawaugh Formation, Surat Basin, Australia	Leederville Formation, Western Australia	Maryborough Formation, Maryborough Basin, Australia	Clent Hills, New Zealand
Age of type formation	Neocomian	Aptian	?Barremian-?Aptian	Aptian	?Bajocian-?Callovian	Neocomian-Barremian	Aptian	?Middle Jurassic

Table 1. Comparison of conifer fossils with similar gross morphology to *Bellarinea richardsii* from Mesozoic sediments of Australia, India and New Zealand. Information from Walkom (1921), Sahni (1928), Florin (1952), Townrow (1968), White (1981), McLoughlin (1996) and McLoughlin et al. (2000).

E. baddowensis (McLoughlin et al. 2000), that is distinguished by its oblong to lanceolate leaves with rounded apices and slightly contracted bases.

Species of *Elatocladus* described from the Yorkshire Jurassic (Harris 1979), although similar in general leaf morphology to *Bellarinea richardsii*, all represent indeterminate shoots and exhibit either branching or buds, both of which are absent from the Boola Boola specimens. Several species of *Elatocladus* described from the Jurassic and Early Cretaceous of Antarctica (Halle 1913, Gee 1989, Cantrill 2000a,b, Cantrill & Falcon-Lang 2001) differ from *B. richardsii* by being branched and indeterminate. Of these, *E. australis* has lateral shoot units subtended by a resting bud of scales, which Cantrill (2000a) suggested may be evidence of deciduousness or at least arrested growth. The latter is most likely given that Cantrill's figure 7.1 shows a shoot of rhythmic growth with large leaves either side of a region of restricted growth

Associated plant fossils.

Bellarinea richardsii is by far the most abundant of the three conifer foliage species in the Boola Boola macroflora, but this may reflect a deciduous habit rather than floristic dominance. The assemblage also contains several other gymnosperms including bennettitaleans (*Otozamites* spp.), pentoxylaleans (*Taeniopteris daintreei* McCoy), and pteridosperms of uncertain affinity (*Rintonlia variabilis*, *Pachydermophyllum austropapillosum* and *Komlopteris indica*; McLoughlin et al. 2002). Ferns are represented by around ten foliage-based species (Douglas 1973) and lycophytes are represented by abundant detached microphylls and 16 species of megaspores (McLoughlin et al. 2002). *Bellarinea richardsii* is most commonly associated with *Taeniopteris daintreei*, *Rintonlia variabilis* and *Otozamites* spp. in floodbasin siltstones and crevasse-splay sands (McLoughlin et al. 2002). Based on their abundance in these sediments, their taphonomy, associated fossils, and previous palaeoecological interpretations of this plant group (Douglas & Williams 1982), *Bellarinea richardsii* is interpreted to have constituted an upper storey tree. It occupied relatively moist floodbasin environments in alluvial valley systems during the initial establishment of the Gippsland Basin rift.

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